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Contributions to the embryology of the Ranunculaceæ.[1]

WITH PLATES XVII–XX.

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Various representatives of the Ranunculaceæ have been subjected to much careful study from the standpoints of morphology, histology and embryology. The well known resemblance to the monocotyledons in the structure of the vascular bundle, secondary growth of the stem and the large size of their meristematic cells, has brought to several species of this family much of that careful investigation that is usually centered upon transitional characteristics. Of all the dicotyledons certain species of the Ranunculaceæ resemble more closely the monocotyledons in the large size of their embryonic cells.[2] For this reason certain species are especially favorable for embryological studies. From a desire to know more about the development of the embryo-sac, a study of one or more species of several available genera was begun.

Prantl[3] arranges the genera of this family under three subdivisions, Paeonieæ, Helleboreæ and Anemoneæ. Of the Paeonieæ no representative was available for study; of the Helleboreæ the following species were investigated: *Delphinium tricorne* Michx., *Caltha palustris* L., *Aquilegia Canadensis* L.; of the Anemoneæ, *Ranunculus abortivus* L., *R. recurvatus* Poir., *R. septentrionalis* Poir., *Anemonella thalictroides* Spach, *Thalictrum dioicum* L. and *Hepatica acutiloba* DC.

The subject naturally embraces three phases, namely; the development of the embryo-sac, the process of fertilization, and the development of the embryo.

The following pages will be confined almost exclusively to the development of the embryo-sac and its behavior previous to fertilization. The different species will be taken up in the order indicated above.

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[1] Contributions from the Botanical Laboratory of the University of Indiana.

[2] Strasburger, Histologische Beiträge 5: 118. 1893.

[3] Natürlichen Pflanzenfamilien.

Delphinium tricorne.—As is well known the ovules of Delphinium arise as nipple-like protuberances from the infolded margins of the carpophyll. The epidermal and hypodermal rows of cells of the carpophyll pass uninterruptedly over this rudiment of the ovule. At the apex of the protuberance may be seen one or frequently more hypodermal cells distinguishable by their larger size (fig. 2). The cell which ultimately gives rise to an embryo-sac will, for greater clearness, be spoken of in this paper as the initial cell of the embryo-sac, while the term mother-cell will be reserved for the lower one of the longitudinal row of cells arising from subsequent divisions of this cell. In the very young rudiment of the ovule (fig. 1) in a large number of cases the initial cell of the embryo-sac is not perceptibly different from the other hypodermal cells nor the cells of the young ovule in general. It is usually stated that the initial cell of the embryo-sac is the terminal one of an axial row of cells of the nucellus, especially in monocotyledons which possess small ovules. In larger, small-celled ovules, those of the dicotyledons particularly, proof of an axial row is indeed difficult, if not quite impossible. In few cases in Delphinium an axial row could be determined (fig. 2); but it is very evident, even in the most favorable cases, that the initial cell or cells sustain a closer genetic relationship with the hypodermal layer than with any other cells of the nucellus (figs. 1–3).

The initial cell now incrcases in size, and divides by a transverse wall into two cells, the lower being frequently a little larger than the upper (figs. 4, 5, 7). When the first division is completed in the initial cell, the epidermal cells of the nucellus have divided by periclinal walls, and the inner integument has attained a level with the apex of the nucellus. Each of the two resulting cells (fig. 5) now divide by a wall parallel to the first, thus giving rise to four cells by two successive divisions of the initial cell of the embryo-sac. These transverse walls are very thin membranes without being the least swollen in the instances figured. As far as observation extended, the division of the lower cell preceded that of the upper, as will be seen in figs. 6 and 7. These divisions follow as a rule in rapid succession. The lower one of the row of four cells now becomes a mother-cell of the embryo-sac. It increases in size, gradually absorbing the three cells above and also the adjacent cells of the nucellus, a process that almost invariably obtains in all angiosperms. In fig. 8 the mother-cell may be seen separated from the disorganized remains of the three superposed cells by an arched wall which is somewhat swollen.

The nucellus here has elongated, so that at this stage of development the three disorganized cells do not appear as flattened caps above the encroaching mother-cell, but seem to form only a narrow cavity containing a structureless substance which stains deeply. I have not been able to show this accurately in the pen drawing. This cavity is made narrow both by the increase in length of the nucellus and by the turgor of the cells immediately surrounding it. The walls of the turgid cells here in question, which border upon the cavity, are usually much swollen. The mother-cell now develops into the embryo-sac in the normal manner. The mature embryo-sac is covered by the nucellar cap varying from two to four cells in thickness. The antipodal cells attain an extraordinary size compared with that of the egg-apparatus, as a glance at figs. 10*a* and 10*b* will plainly show. This condition of affairs exists in the embryo-sac at the time of anthesis or shortly before. The three cells almost always lie side by side in the same horizontal plane, consequently only two are shown in the figure, the other being in the next successive section. They gradually increase in volume with the subsequent growth of the embryo-sac, and persist for a time after fertilization, when they are finally absorbed. About the time of fertilization they may be seen upon a projection of the chalaza at that end of the sac which has now become very broad. However, the position of the antipodal cells varies considerably in different ovules. Strasburger has called attention to the enormous size of the antipodal cells in *Delphinium villosum.*[4] In Delphinium tricorne the writer did not find the difference to be quite so great. We shall return to this phenomenon further on.

The only account of the development of the embryo-sac in any representative of the Ranunculaceæ to which I have access is that given by Strasburger[5] for *Myosurus minimus.* In this plant the author finds that the initial cell gives rise to a row of only three cells, the lower one of the series developing into the embryo-sac in the normal way. It will be seen that Delphinium differs from Myosurus in that four cells result from two successive cell divisions of the initial cell, of which the lower one gives rise directly to the embryo-sac. It is not improbable, however, that occasionally only three cells are formed here as in Myosurus, a phenomenon that was observed in other genera to be mentioned later.

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[4] Strasburger, Ueber Befruchtung und Zelltheilung 38. 1878.

[5] Strasburger, Die Angiospermen und Gymnospermen 13. 1879.

The most remarkable phenomenon met with here is the presence of two and sometimes more initial cells and their development into mature embryo-sacs. In figs. 1 and 3 may be seen two initial cells of about equal size. In a number of cases one of the cells was somewhat larger than the other. The larger would in all probability take the upper hand of the smaller, thus crowding it out when only one embryo-sac would be the result. Frequently two cells were observed in later stages of development (fig. 7), both of which would, without doubt, produce mature embryo-sacs. As a rule one cell is a little in advance of its neighbor in development (fig. 7, the cell on the left). This state of things is not exceptional, but in some carpels a large number of ovules presented two, and occasionally three, initial cells. It is certain that every initial cell does not ultimately result in a mature embryo-sac, for it seems that there is unquestionably a "struggle of the parts" here as elsewhere. No more than two embryo-sacs were observed in one ovule. In fig. 9 are shown two fully developed embryo-sacs, apparently of equal size and importance. The antipodal cells lie side by side in a plane at right angles to the plane of the section. By focusing deeper other nuclei could be seen, and in an adjacent section the other antipodal cells were visible. The two embryo-sacs were contiguous for their whole length, separated only by a very thin and indistinct membrane. For lack of time a very large number of ovules was not examined to ascertain the frequency of the phenomenon, nor is it known to the writer whether more than one embryo-sac is fertilized, and in that event whether more than one embryo ever reaches maturity in a single seed of Delphinium.

We do not have to do here with an isolated phenomenon, for the presence of more than one embryo-sac in one ovule has been observed several years ago by Hofmeister,[6] Tulasne, Schacht and others.

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[6] Strasburger, Ueber Befruchtung und Zelltheilung 36 and foot note.

Tulasne claims to have observed five or six embryo-sacs in a single ovule; but it is probable that the methods used in the preparation of objects by earlier observers were less accurate than those employed by more recent investigators, consequently such statements may be reasonably questioned. The most remarkable instance, however, is that noted by Strasburger[7] for *Rosa livida.* I quote from this author as follows: "Im fertigen Zustande sah ich die Embryosäcke stets in Mehrzahl den Eichenkern durchsetzen, sich nach hinten und im grössten Theile ihres Verlaufs unmittelbar an einander haltend, um erst mit den vorderen Enden zu divergiren. Hier aus einander weichend wachsen sie in das umgebende Gewebe hinein (taf. VII, fig. 72), meist dringt einer bis zu den Integumenten vor, und dieser führt dann auch allein den aus drei Zellen bestehende Eiapparat, während es in den anderen bei einer Ansammlung formlosen Protoplasmas im vorderen Ende bleibt." In Delphinium, as previously stated, the two sacs are in contact for their entire length. The egg apparatus in each is normal and apparently well developed. Here the embryo-sacs are always covered by the nucellar cap, even after fertilization. The writer has seen in one case two embryo-sacs in *Senecio aureus*, and two in process of development in *Fagus ferruginea.*[8] The same has also been observed in *Fagus sylvatica.*[9]

Caltha palustris.—This species presents a number of interesting phenomena in the larger number of initial cells of the embryo-sac frequently met with and their subsequent behavior. The structure and development of the ovule is the same as in Delphinium, except the larger size of its cells, especially those connected either directly or indirectly with the reproductive function. The initial cell of the embryo-sac is hypodermal, sustaining a closer genetic relation apparently to this layer than to the more centrally situated cells of the nucellus. Here, however, a greater number of initial cells are present, forming in many cases what seems to be a massive archesporium. Sometimes three rather large initial cells may be seen in a longitudinal section of the ovular rudiment (fig. 11), and occasionally four or more forming a small group of cells more loosely arranged (fig. 12). The latter state of things was observed in one case only. Frequently only one initial cell could be seen, yet two were usually present. The initial cell divides by a transverse wall into two unequal cells, the lower being the larger (fig. 13). Very soon a division takes place in the lower cell (fig. 14) thus giving rise in all to three cells. It can not be said with certainty that this is always the order of division, but in the particular instances figured, there can be little doubt, for in fig. 13 the nucleus of the lower cell is in the skein stage of the prophases. In fig. 14, it will be observed that the middle cell is somewhat compressed by the enlarging mother-cell of the embryo-sac. Sometimes, however, the first division wall in the initial cell is inclined at an angle of about forty-five degrees; in other cases it was greatly arched downwards, *i. e.*, away from the apex of the nucellus, making the upper cell the larger; again a division may take place in the nucleus of the upper cell without being followed by cell-division (fig. 19). All this may take place before any sign of an integument is visible. In fig. 15 it is clear that cell-division did not follow nuclear division in the lower cell resulting from the first division of the initial cell. The two nuclei lie in opposite ends of the cell, separated by two large vacuoles. From the fact that growth is here very rapid, it may be suggested that the forces controlling nuclear division and the formation of the new cell wall were proportionately weaker than those which, at the same time, bring about the growth in size of the dividing cell. Usually the lower cell of the three becomes the embryo-sac, as in the vast majority of phanerogams, but the uppermost cell of the row may probably become the mother-cell of the embryo-sac (fig. 16). Of course, it is impossible to state definitely what would be the final result of such a condition here figured, as it was the only instance of the kind observed. The lower cell which is slightly disorganized is partly hidden by the cell above it, which in turn is somewhat overlapped by the terminal cell of the row. In this ovule the inner integument has just begun its development.

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[7] Ueber Befruchtung und Zelltheilung 36.

[8] My paper, of which this species forms a part, is now in preparation.

[9] Benson, Margaret, contributions to the embryology of the Amentiferæ. Trans. Linn. Soc. Bot. II. **3:** 409–424.

The mother-cell now develops rapidly into the embryo-sac. In fig. 17 will be seen such a cell with the remains of the disorganized cells above it. The large cell just beneath this is evidently one of the axial row of the nucellus, which failed to divide, and has become, as a result, larger than the neighboring cells of the nucellus. Fig. 18 presents a sac with two nuclei in each end. The outer integument has now put in an appearance on the side turned from the funiculus (on the right in the figure), and the epidermis of the apex of the nucellus has given rise by periclinal divisions to a layer of three or four cells in thickness. This layer may be formed earlier in the development of the ovule (fig. 17). The embryo-sac is not infrequently mature when the inner integument has reached the apex of the nucellus. In regard to this point there is considerable variation, for both integuments may exceed the nucellus before the maturity of the embryo-sac.

The embryo-sac presents nothing abnormal. In the antipodal cells, which become quite large, the nuclei undergo fragmentation, so that each cell at the time of anthesis, contains three or four nuclei.

On account of insufficient material only a limited study of the mature sac was made. In all cases examined only one embryo-sac was found in each ovule, yet the probability is not excluded that more than one may reach maturity as in Delphinium.

Aquilegia Canadensis.—This genus, in the species investigated, presents variation in the behavior of the initial cell of the embryo-sac, along a line different from either Delphinium or Caltha. It may be stated first of all that the most striking histological phenomenon here is the smallness of the cells and consequently the small dimensions of the young ovules as compared with those of the preceding genera.

The initial cell which, of course, is hypodermal in origin, is distinguished from its neighbors of that layer only after a marked increase in size. With the growth of the nucellus it increases perceptibly in length accompanied by a similar growth in the adjacent hypodermal cells, and, in several instances observed, cuts off a small cell from the top, which seems to be a tapetal cell (fig. 20). The lower and larger cell now divides transversely (fig. 21), each of the resulting cells dividing in a similar way (fig. 22). More frequently, however, no such tapetal cell is formed, the initial producing a series of four cells in the manner described for Delphinium (figs. 23, 24). In fig. 23 the upper cell has just divided. The transverse walls are very delicate and the nuclei poor in chromatin, facts which seem to indicate that the two divisions followed in rapid succession. The lower cell (fig. 24) has increased in size apparently by keeping pace with the elongation of the nucellus, as the cross wall separating it from the cell above is horizontal. Its nucleus is a little larger than those of the cells above, and a large vacuole occupies the upper third of the cell.

In fig. 25 it is evident that five cells have been formed from the initial cell. It is quite impossible to determine the exact order of cell-division in this case. It may have been in the manner indicated in figs. 20, 21, and 22, or the uppermost cell of the four resulting from the two successive cell-divisions (fig. 23 or 24) may have undergone a further division. Judging from my experience in this work and the appearance of the preparation from which fig. 25 was drawn, I am inclined to regard the latter process as the correct one. The condition presented by fig. 26 seems to support this view, for there can be little doubt that the uppermost cell of the series divided again at almost right angles to the usual plane of division.

The mother-cell now develops in the usual manner. When the nucellus, by lateral pressure and growth, becomes more elongated, the space occupied by the remains of the disorganizing cells is almost obliterated by the turgor of the surrounding cells (compare figs. 27 and 28). The mother-cell continues its growth mainly at the expense of the cells in front of it, and when it has reached the epidermis, whose cells have now been doubled by periclinal divisions, a nucleus occupies each end with a large vacuole between them. The further development is perfectly normal.

In the newly formed embryo-sac the antipodal cells, which are always surrounded by very evident membranes, taken together have about the same volume as the egg-apparatus (fig. 29). With the gradual increase in size of the embryo-sac prior to fertilization and some time afterwards, the antipodal cells become enormously enlarged, being very rich in protoplasm, with numerous vacuoles especially in their broad upper ends. The nuclei multiply by fragmentation.

A glance at fig. 30*a*, a small embryo with a cell by its side, probably one of the synergidæ, and fig. 30*b*, two antipodal cells taken from the same embryo-sac, will give one some idea of the phenomenon just mentioned. In this embryo-sac the endosperm consisted of many free nuclei regularly disposed in the protoplasmic lining of its cavity, *i. e.*, the endosperm is a single layer of free cells.

(To be concluded.)